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Pleistocene Speciation in Amazonian Birds ¹⁾

by

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Introduction

In studying low latitude faunas we distinguish between ecological and historical aspects of increased species diversity or between attempts to explain maintenance and origin of tropical species diversity. High numbers of closely packed sympatric species and their interrelationships in a tropical forest pose problems to the ecologist who investigates the functioning of complex ecosystems. We are here concerned with an historical analysis of the Amazonian bird fauna or with the question of "How did the numerous tropical species originate?" In an approach to this problem I used several methods to differentiate geographically the rather uniformly forested lowland regions of central South America and their bird faunas. I mapped regional variations in annual rainfall, the location of avian distribution centers, and the location of contact zones where members of avian species and subspecies pairs met in the recent geological past. I then interpreted the results of these studies on distribution patterns and population structure of selected groups of Amazonian birds in the light of palynological and geomorphological findings regarding the Quaternary climatic and vegetational history of tropical South America. Briefly, vast changes in the distribution of forest and nonforest vegetation and their faunas occurred as a result of repeated climatic fluctuations during the last 800 000 years. Numerous tropical forest birds probably originated from small isolated populations that survived adverse climatic phases in restricted forest refugia. Pleistocene species multiplication in low latitudes seems to have followed the orthodox process of geographic speciation. The species generated in large numbers met in re-expanding forests during humid periods and often are able to coexist through niche reduction and specialization under the comparatively stable or at least less demanding ecological conditions of tropical forests, in this way gradually building up, from simpler Tertiary faunas, the surprising species diversity observed in Amazonia today.

We may first summarize briefly the presently available evidence of alternating arid and humid Pleistocene climatic periods which greatly influenced the faunal differentiation in central South America during this epoch. A more detailed review of this data and of my ornithological interpretations has appeared in a recent monographic study on "Avian speciation in tropical South America" (HAFFER 1974).

Quaternary Climatic and Vegetational Changes in Tropical South America

Palynological studies of lake and bog deposits as well as geomorphological investigations in various parts of northern and central South America indicate that the Pleistocene climatic fluctuations severely affected not only the higher levels of tropical mountains but also the surrounding lowlands (study areas are marked on Figure 1). Although temperatures during cold phases probably remained high in the tropical lowlands where the cooling may have reached only 3 to 4°C, the alternation of humid and arid periods led to drastic changes in the distribution of forest and nonforest vegetation. Forests were probably reduced to a number of comparatively small remnants during dry phases when the nonforest vegetation became widespread. During the humid periods which followed, the forests re-expanded and often rejoined to form large extensive forests, in this way isolating remnants of the previously more continuous open savanna areas.

Van der HAMMEN (1968, 1972, 1974) and his associates documented Pleistocene and post-Pleistocene climatic and vegetational changes in the Colombian Andes and surrounding lowlands, e.g. in the lower Rio Magdalena Valley (E of Fig. 1) and in the Llanos plains (V of Fig. 1) as well as in the Guianas (G and R of Fig. 1; WIJMSTRA 1967, WIJMSTRA et al. 1966, BAKKER 1970, KROOK 1970, Van der HAMMEN et al. 1973). According to GARNER (1966), the gravel deposits, river channels, and land forms of the Rio Caroní drainage system in southern Venezuela (C of Fig. 1) can best be explained in terms of several alternating humid and arid climatic periods. The same applies to the Amazonian foothills of the Peruvian Andes (P of Fig. 1; GARNER 1959). Recent palynological data of bore hole samples from Katira Creek, 120 kilometers southeast of Porto Velho on the upper Rio Madeira (O of Fig. 1), indicate that in this area the tropical rainforest was temporarily replaced by open savanna vegetation, presumably during portions of the Pleistocene (Van der HAMMEN 1972, ABSY and Van der HAMMEN 1977).

The only geologic study of Quaternary sediments in the Amazon Valley itself near Manaus (M of Fig. 1; MOUSINHO 1971) also favors the interpretation of a changing vegetation cover under varying climates in central Amazonia. Further studies in lower Amazonia and in the upper Rio Branco Valley have been summarized by VANZOLINI et al. (1970), Van der HAMMEN (1974), and critically reviewed by FITTKAU (1974). Extensive geomorphological studies were conducted by BIGARELLA et al. (1965) in eastern and northeastern Brazil (B of Fig. 1). Evidence for alternating climatic cycles is also available from the offshore region of eastern Brazil (DAMUTH et al. 1970, 1975) and from the presently arid Pacific slope of the Peruvian Andes (L of Fig. 1; GARNER 1959, LANNING et al. 1967). HAFFER (1974) and SIMPSON (1975) reviewed the results of additional paleoclimatical investigations in the tropical Andes.

Although the study areas mentioned above are widely scattered over the vast lowlands of tropical South America, all authors agree in their basic conclusion that drastic changes in climate and vegetation have taken place in the recent geologic past. More detailed investigations are needed especially in the central and upper Amazonian lowlands which remain largely unexplored in this regard. In particular, no direct palynological evidence of continued forest growth in the presumed refuge areas during the Pleistocene is available as yet. The few studies so far carried out in Amazonia refer to regions between the refugia.

The absolute age of the various climatic periods, their varying intensity over different parts of South America, and their correlation in the Andean and extra-Andean regions remain to be investigated. During part of the glacial advances, the Andes had a humid climate which, however, turned very arid during the peak of glaciation (Van der HAMMEN 1974). These periods may have coincided with the dry phases in the lowlands east of the Andes. The last severe arid period which probably led to a separation of lower and upper Amazonian forests occurred during the interval 4000 to 2500 years ago (BIGARELLA 1965). Forests re-expanded during the following humid period which extends to the present time and led to the isolation of nonforest animal populations on the presently remaining savanna enclaves within the Amazonian forests.

Pleistocene Speciation in Amazonian Birds

The severe reduction of forest growth during arid climatic periods of the Pleistocene presumably did not affect the neotropical lowlands uniformly. Forests probably survived

in more or less restricted humid areas which served as "refugia" for the Amazonian forest faunas. Differentiation of isolated populations took place in these forest refugia due to varying selection pressure, chance, and the varying "plasticity" of systematic units following the model of geographic speciation (MAYR 1942, 1963). Wide dispersal of nonforest animals occurred during periods of forest reduction, thus explaining the close relationships between northern and southern neotropical nonforest species presently separated by the entire width of the Amazonian forest. Re-expanding forests during humid periods led to the retreat of the nonforest vegetation and its associated fauna and to the isolation of some species on savanna enclaves which remained within the Amazonian forest.

I used the following criteria to establish tentatively the location of fifteen forest refugia (dispersal centers) or groups of refugia in tropical South and Central America during repeated arid climatic phases of the Pleistocene (HAFFER 1967a, 1969, 1974, 1975): Rainfall centers, avian distribution centers (core areas), the location of secondary contact zones as well as the results of geomorphological and palynological studies reviewed above. This approach combines aspects of the more geographically oriented method of mapping distribution centers (REINIG, de LATTIN; MÜLLER 1973, for South America) with the approach of the "speciationists" who study the relationships and history of differentiation of taxa that are either allopatric or meet along zones of secondary contact (VUILLEUMIER 1975: 431).

Rainfall centers.

Conspicuous regional variation in the distribution of annual rainfall in Amazonia is mainly determined by the relief. Mountain slopes force air masses to rise resulting in increased precipitation and causing a rain shadow effect on the leeward side. Since the basic features of the South American relief had been established at least in early Pleistocene time, the assumption seems justified that, during arid climatic periods, forests disappeared first from areas presently receiving relatively little rainfall and survived in centers with the greatest precipitation. Rainfall centers receiving over 2500 millimeters of rain per year are located in upper Amazonia near the base of the Ecuadorian and Peruvian Andes, along the Atlantic slope of the Guianas including the mouth of the Amazon river, along the Andean foothills of northern and western Colombia and along the Middle American mountains (Fig. 1). Among the less humid areas between rainfall centers, the "dry transverse zone of lower Amazonia" is especially noteworthy (REINKE 1962). It connects the nonforest regions of northern and central South America and is characterized by a long and rather severe dry season in contrast to upper and lower Amazonia to the west and east. Numerous isolated savannas within uniform forests occur within this "dry transverse zone" and characterize this region as transitional between forest and nonforest vegetation, although forests predominate at the present time (Fig. 1).

Avian distribution centers.

The comparative study of species ranges leads to the recognition of geographically-ecologically related and presumably also historically related species. By superimposing the range outline maps of species of a given region, centers of distribution of core areas (nuclear areas, Arealkerne, Kernareale) are recognized which all member species inhabit. If no major geographical shifts or other disturbances have occurred, the centers of origin of the species groups considered may be located somewhere within the present core areas or, in simple cases, the core areas themselves may represent the centers of differ-

entiation from which radial expansion has taken place. Distribution centers have been analysed and used in their interpretations by several authors working on the faunas of the Palearctic Region, North America and Africa, as summarized by UDVARDY (1969: 283 ff.).

The following distribution centers emerged from an analysis of the distribution pattern and population structure of nearly 300 neotropical lowland forest bird species which represent about half of the forest bird fauna of Amazonia (HAFFER 1967a, 1969, 1974):

I. Trans-Andean centers

- Caribbean Middle American centers (Guatemala, Costa Rica)
- Pacific Middle American center (Costa Rica)
- Pacific Colombian center (Chocó center)
- Nechí center
- Catatumbo center

II. Cis-Andean centers

- Napo center
- Eastern Peruvian centers
- Madeira-Tapajóz center
- Imerí center
- Guiana center
- Belém center
- Serra do Mar centers

Main core areas or primary distribution centers of the cis-Andean lowlands are the Napo center and the eastern Peruvian centers in upper Amazonia (Fig. 2). With the exception of the somewhat more weakly expressed Belém center, each of these core areas is nearly as important zoogeographically as the humid forests of Atlantic southeastern Brazil (Serra do Mar centers), which remain separated from the Amazonian forests by the dry tableland of central and northeastern Brazil. Additional distribution centers (secondary centers) in the Madeira-Tapajóz and Imerí regions of central Amazonia are of secondary importance and need further investigation.

The ranges of a number of bird species and subspecies are limited by broad Amazonian rivers, especially the lower Rio Amazonas and the lower portions of the Rio Negro, the Madeira and Tapajóz Rivers (Fig. 2). However, some of these birds are in broad contact in the headwater region where these rivers cease to function as barriers. The overall significance of Amazonian rivers as limiting barriers appears to be rather restricted when a large sample of species and subspecies ranges is compared. Further aspects of avian distribution patterns in central South America are discussed by HAFFER (1974, 1977).

Secondary contact zones.

Secondary contact zones of Amazonian forest birds indicate the previous existence of ecological barriers between populations presently in contact, although the barriers themselves have since disappeared. Contact zones fall between distribution centers (core areas), thus supporting our interpretation that these centers have functioned in the past as forest refugia and dispersal centers. Because of the varying rate of differentiation in different species, the populations that came into contact had reached many different levels in the speciation process. Weakly differentiated populations hybridized extensively. Other populations may have developed morphologic, behavioral and/or ecological differences

during one or more periods of isolation so that, upon re-establishing contact in re-expanding forests, hybridization was reduced or did not take place at all. Range overlap resulted in sympatry if the allies had reached sexual as well as ecological isolation. In a number of cases, the allies in contact do not hybridize or do so only very rarely, yet remain parapatric, i.e. exclude each other geographically in fairly uniform forest presumably as a result of ecological competition¹⁾. Some of these parapatric species might be expected to overlap their ranges maintaining interspecific territories. Why this is not achieved more frequently remains unknown. Detailed field studies of all contact zones and especially of competitive interactions of parapatric allies in Amazonia are desirable, as the results would add to our understanding of the ecology and interrelationship of tropical forest birds in general. A number of birds like manakins, jacamars and toucans are common enough to make such studies feasible.

Numerous zones of secondary contact of forest birds are clustered in several well defined areas of Amazonia (HAFFER 1974) indicating that here entire faunas overlapped and partly fused ("suture zones" of REMINGTON 1968). An example of a zone of faunal intergradation is the northcentral Amazonian suture zone in southern Venezuela and northern Brazil (Fig. 9). Numerous upper Amazonian and Guianan species and subspecies have here established contact. Close to the Amazon River, the wide lower Rio Negro separates the western and eastern forms. Fusion of the upper and lower Amazonian faunas is less localized south of the Amazon River. Contact zones are here correspondingly scattered over a wider area. Suture zones are developed south of the upper Amazon where eastern Ecuadorian and eastern Peruvian forms are in contact as well as west of the Andes in Honduras-Nicaragua and in Panamá-northwestern Colombia (HAFFER 1975). In the latter area, Pacific Colombian species established contact with Middle American allies or with Amazonian forms that had come around the northern Andes via the Caribbean lowlands of Venezuela and Colombia.

An example of a zone of secondary intergradation in central Amazonia is the hybrid zone between upper and lower Amazonian forms of the black Channel-billed Toucan (*Ramphastos vitellinus*, Figs. 3 and 4). Differences in the color of the throat and upper breast, of the uppertail coverts, bill, iris, and facial skin distinguish three geographical subspecies in upper Amazonia (*R. v. culminatus*) and in lower Amazonia north and south of the Amazon River (*R. v. vitellinus* and *R. v. ariel*, respectively). I analysed this hybrid zone by determining and contouring the character index values of the sample populations (Fig. 3; see HAFFER 1974 for details). Characters used in this study were given the numbers 0 and 3 in phenotypically pure specimens of the hybridizing subspecies and the numbers 1 and 2 in intermediate stages. In each specimen, the values for the characters treated in this way were determined and totaled to arrive at the character index or hybrid index. The mean hybrid indices of the sample populations were then determined and plotted on a map of South America.

Highly variable hybrid populations inhabit the forests of central Amazonia in areas where the eastern forms *vitellinus* and *ariel* met the western *culminatus* in the recent geologic past. Hybridization takes place over a fairly narrow zone in southern Venezuela, where comparatively small populations met in restricted valleys. Therefore, massive introgression is prevented. The broad lower Rio Negro also hinders gene flow conspicuously resulting in nearly "pure" populations of *culminatus* and *vitellinus* occupying the western and eastern bank near the river mouth, respectively. A similar barrier effect of the southern tributaries, Rio Madeira and Rio Tapajoz, is seen on the map (Fig. 3) and diagram (Fig. 4) of this hybrid zone. Whereas a steep continuous intergradation is developed in southern Venezuela, the

hybrid zone is conspicuously segmented in the area of the broad southern tributaries of the Amazon River probably because of more restricted gene flow. The barrier effect of these rivers ceases farther south going upstream and the hybrid zone swings eastward across the narrower upper Rio Tapajoz and Rio Xingú. Hybridization between respective populations occupying the northern and southern bank of the lower Rio Amazonas is prevented by the isolating effect of this wide river course. However, the Guianan form *R. v. vitellinus* and the populations of *R. v. ariel* are potentially interfertile, as both hybridize extensively with *R. v. culminatus* of upper Amazonia.

A similar hybrid zone in central Amazonia is developed in the large White-throated Toucan, *Ramphastos tucanus* (Fig. 5) which resembles *R. vitellinus* in its predominantly black plumage color but differs strikingly in its far-carrying yelping song. *R. tucanus* inhabits all of Amazonia but did not reach the coastal forests of southeastern Brazil. The bill is laterally black and the uppertail coverts are sulphur yellow in the populations of upper Amazonia (*R. t. cuvieri*) whereas these parts are colored dark red and pale lemon yellow, respectively, in the populations of northeastern South America and around the mouth of the Amazon (*R. t. tucanus*). Phenotypically intermediate and highly variable populations form extensive hybrid zones in southern Venezuela and in the valley of the lower Rio Negro. South of the Rio Amazonas, hybrid populations are found between the Madeira and Tocantins Rivers (Fig. 5). Intermediate bill color was scored 1, 2, 3 or 4 according to the extent to the red bill color. Zero designates uniform black sides of the bill (*cuvieri*) and 5 to 6 refers to more or less uniform red or orange red lateral surfaces of the bill (*tucanus*); see HAFFER (1974) for further details.

The northern hybrid zone becomes very narrow in the valley of the lower Rio Negro probably because this wide river course represents a rather effective barrier and consequently reduces geneflow between the eastern and western populations. The same applies to the lower Amazon River which separates pure *tucanus*-populations on the northern bank from highly variable hybrid populations south of this river. The bill is extensively black in the populations inhabiting the valley of the lower Rio Tapajoz where the length of the red stripe or spot on the lateral surface of the bill varies between 2 and 5 centimeters but increases in size rapidly in the populations between the Xingú and Tocantins Rivers to the east. A gradual decrease of mensural characters is observed as one moves from eastern Ecuador (*cuvieri*, wing 251 mm, bill 183 mm) eastward along the Amazon Valley to the Atlantic coast (*tucanus*, wing 235 mm, bill 163 mm).

A comparison of the hybrid zones found in the smaller Channel-billed Toucan (*R. vitellinus*, Fig. 3) and in the larger White-throated Toucan (*R. tucanus*, Fig. 5) reveals similarities as well as differences. The situation is very similar in northern Amazonia where contact of an upper Amazonian and a Guianan population was established in both cases in southern Venezuela. The mountainous terrain in this region (Roraima table mountains) and the barrier effect of the lower Rio Negro determined gene flow in *vitellinus* and *tucanus* in the same manner, thus leading to almost identical shape, width and location of the hybrid zones north of the middle Amazon River, although westward introgression of the Guianan characters is somewhat more pronounced in *R. t. cuvieri* than in *R. v. culminatus*. Differences of the hybrid situations in these toucans are prominent in southern Amazonia. In the larger species, the upper Amazonian *cuvieri* was able to extend its range eastward to the Tapajoz-Xingú region mainly because no representative existed in the Belém region near the mouth of the Amazon and *tucanus* was held up by the broad lower Rio Amazonas. On the other hand, the presence of an additional representative of *vitellinus* in eastern Amazonia (*ariel*) determined the location of the hybrid zone in this species in northcentral Brazil.

In contrast to the examples among toucans discussed above, other cases are known where relatives come into contact in uniform Amazonian forests but do not hybridize, probably excluding each other as a result of ecological competition. These allies appear to have reached sexual isolation prior to establishing contact yet remained sufficiently competitive to hold each other off. Taxonomically, these relatives are allospecies together forming a superspecies. Although no detailed field studies have been carried out, this interpretation probably applies to the following parapatric species in Amazonia (Fig. 6): The cotingas *Phoenicircus nigricollis* - *P. carnifex*; *Xipholena punicea* - *X. lamellipennis* - *X. atropurpurea*; the manakins *Pipra filicauda* - *P. fasciicauda* - *P. aureola*; and the tanagers *Euphonia rufiventris* - *E. cayennensis* - *E. pectoralis*. Except for the manakins, these are strong-flying

1) Allopatric populations also occupy mutually exclusive areas but are not in geographical contact. Therefore, the decision whether closely related allopatric populations are still subspecies or have reached the species level of differentiation in many cases will be highly subjective.

members of the canopy fauna and travel large distances between fruiting trees. HAFFER (1970, 1974) discussed these as well as other superspecies among Amazonian parrots, toucans, trumpeters, and jacamars (Figures 7 and 8).

Member species of Amazonian superspecies occupy large areas of rainforest and replace each other abruptly along sharply defined contact zones. The degree of control in the form of specimens collected, of course, varies considerably in the different species and in different portions of Amazonia. Occasional hybridization may occur locally (and has actually been found in the species of *Pipra*, HAFFER 1970) but continuous zones of intergradation certainly do not exist in the cases mentioned above. In order to explain this situation, it appears necessary to postulate the origin of the various closely related allospecies from small ancestral populations during one or more previous periods of geographic isolation and, following later range expansion, the establishment of geographic contact without overlap of the ranges. Occasionally, the contact zone of two allies stabilized locally along broad rivers which represent partial barriers to dispersal (see above). Thus the lower Amazon separates the allies of *Xipholena* and *Euphonia*, and the lower Rio Negro and Rio Tapajóz separate the allospecies of *Phoenicircus* (Fig. 6). In many other instances no relations exist between range limits and river courses in Amazonia.

Forest refugia.

Using the above indirect evidence derived from rainfall inequalities, from the location of avian distribution centers and suture zones between such centers as well as the results of geomorphological and palynological investigations in the Neotropics, I reconstructed the probable geographic location of fifteen Quaternary forest refugia or groups of refugia in the lowlands of Middle and South America (HAFFER 1967a, 1969, 1974). They are named and mapped in Figure 9. The areas designated as Pleistocene forest refugia are presently characterized by lush forest growth in the lowlands around or along steep hills or mountains exposed to moisture laden winds and are inhabited by numerous animal species of restricted geographical range. Mountain slopes above postulated lowland refugia were probably also humid and forested, thus serving as refugia for montane forest species. Additional Andean forest refugia probably existed in humid pockets and were unrelated to the lowland refugia. This is the case in the forest refuges on the upper slopes of the southern Venezuelan table mountains, where montane forest birds probably survived arid climatic periods in the absence of extensive tropical forests in the surrounding lowlands.

Direct field evidence for the former existence of the postulated forest refugia is not yet at hand, as mentioned above. Future palynological studies and geomorphological investigations may indicate the continued growth of forest in regions designated as "refugia" in contrast to areas between forest remnants where savanna vegetation predominated temporarily during the Pleistocene. Presently, statements as to the possible size and shape of the forest refugia during the various dry climatic periods and ecological conditions within the refugia are speculative. Even when field data from Amazonia become available it will remain difficult to map the distribution of forest and nonforest vegetation at any given time under the constantly changing climatic conditions of the Quaternary.

Evidence from studies on other Amazonian animals and on plants.

Animals.

The following results regarding the biogeography of Amazonian reptiles, butterflies, flies, and mammals strongly support our interpretations of the Pleistocene changes and differentiation of the Neotropical bird fauna. In an analysis of the population structure of the widespread South American lizard *Anolis chrysolepis*, VANZOLINI et al. (1970) mapped several areas

of uniform character expression in the Amazonian range of this species that are separated by zones of hybridization and introgression. These authors interpreted this situation as due to secondary intergradation of populations that had been differentiated in geographic isolation during periods of forest reduction. Forest refugia which VANZOLINI (1970) reconstructed for *A. chrysolepis* in tropical South America coincide closely with those proposed by HAFFER (1969, 1974) for Amazonian birds (Fig. 10). Some differences such as the presence or absence of a differentiation center at the eastern base of the Colombian Andes (not indicated by birds) are very minor considering the wide area of agreement.

Other herpetologists also accepted the notion of the origin of numerous species and subspecies of Neotropical frogs, lizards, and snakes in Pleistocene forest refugia discussing the distributional history of these animals relative to Quaternary climatic and vegetational shifts; e.g. DUELLMAN (1972), HEYER (1973), DUELLMAN et al. (1974) and SILVERSTONE (1975) on certain Amazonian frogs, GALLARDO (1972) on the South American amphibian faunas generally, ECHTERNACHT (1971) on Middle American *Ameiva* lizards, HOOGLMOED (1973) on lizards of Surinam, and C. MYERS (1973, 1974) on snakes of the genera *Saphenophis* and *Rhadinaea*.

In studying the geographical variation and mapping the hybrid zones of the various Neotropical forms of the colorful butterflies *Heliconius melpomene* and *H. erato*, TURNER (1971:254) concluded that "the distribution of races in these species is most readily explained as a result of subspeciation occurring as a result of the isolation of populations during climatic cycles accompanying glacial periods.... Subsequent spread of races would result in the polymorphic hybrid areas which we see today...." (see BROWN et al. 1972 for details of the hybrid zones). TURNER (l.c.) also feels that full speciation with secondary range overlap of related forms occurred repeatedly in *Heliconius* during the Pleistocene and led to the complex pattern of diverse, related and mimicking species in this genus. The forest refugia reconstructed by the above authors (BROWN et al. 1974, BROWN, 1975) for the differentiation of various subspecies of *Heliconius* species coincide closely with those proposed for birds (Fig. 10). A somewhat larger number of forest refugia is postulated for butterflies than for vertebrates, possibly because insects survived and were differentiated in a smaller forest remnants than vertebrates, e.g. birds, could.

Moths of the family Sphingidae are widely distributed in submontane and montane forests of the Neotropical Region. Therefore, dispersal centers reconstructed for this family and area by SCHREIBER (1973) are located mostly along mountain ranges.

SPASSKY et al. (1971) summarized the known geographical distribution of six sibling species of the *Drosophila willistoni* group and of six semispecies of the *D. paulistorum* complex. They concluded that the various species and semispecies very likely originated in Pleistocene forest refugia as reconstructed for Neotropical birds. WINGE (1972) is of the same opinion, adding that the pattern of subspeciation in other forms of *Drosophila* also suggests a differentiation in forest refugia.

The distribution patterns of various groups of related Amazonian mammals as well as the location and nature of secondary contact zones suggest to me that the latest differentiation of these animals also occurred as a result of geographical isolation of restricted populations in Pleistocene forest refugia as described above. Examples are cis- and trans-Andean marmoset monkeys (genus *Saguinus*), howler monkeys (genus *Alouatta*), the Capuchin monkeys of the *Cebus albifrons* superspecies, and the South American tapirs *Tapirus terrestris*

and *T. bairdii*, which are in secondary contact in northwestern Colombia (see HAFFER, 1974, for additional discussions and TUTTLE, 1970, for zoogeographical data on Peruvian bats). With respect to tropical Africa, KINGDON (1971: 67) stated "with confidence that past climatic changes, repeatedly isolating and then reuniting the forest areas... have been a major mechanism in the speciation of forest mammals. Monkeys, duikers, squirrels and other rodents show morphological differences that frequently coincide with the forest refuges".

Analysing the distribution patterns of a variety of Neotropical vertebrates, MÜLLER (1972a, 1973a, b) arrived at a zoogeographic subdivision of Amazonia and an interpretation of the Pleistocene differentiation of its fauna similar to those of other authors discussed above. Amazonian "dispersal centers" are only broadly defined by MÜLLER who, unfortunately, did not describe details of his method of delimiting the various regions designated as "centers", especially in the cis-Andean lowlands where many of his forest and nonforest centers are adjacent to one another and hardly separated by narrow corridors.

Since MÜLLER's book (1973a) will be widely used, I may mention a few aspects of his study with which I disagree. The use of "subspecies" for zoogeographic studies without qualifications appears questionable. The "subspecies" as such is not a unit of evolution (MAYR 1963) and, therefore, is not a useful category in the analysis of the history of a given fauna or systematic unit, unless a previous study of the population structure of a given species yielded evidence of differentiation during a period of former geographical isolation. Although MÜLLER is aware of this problem, he nevertheless used numerous "subspecies" without discussion in defining dispersal centers. The nature of these "subspecies", however, remains unknown to the reader. I also disagree with MÜLLER's assertion (p. 184) that "populations, as soon as they are specifically distinct, can occur sympatrically alongside other specifically distinct populations". Numerous parapatric bird species in Amazonia, e.g. members of superspecies, exclude each other geographically in uniform forests presumably as a result of ecological competition. A number of unsubstantiated statements in MÜLLER's book may only concern ornithological readers, e.g. the alleged clinal variation of *Galbula galbula* toward the Amazon-Solimões region (p. 74, 87) where this bird is unknown, or the alleged occurrence of certain species of birds in the Manaus area where they have not (yet) been recorded (p. 86; *Pteroglossus flavirostris*, *Galbula ruficauda*, *Pionopsitta caica*, and *Phlegopsis erythroptera*; *Crax rubra* in this diagram should read *Crax alector*). Most of the faunal elements of the North Andean centre are members of primary South American or expanding South American bird families rather than "of North or Central American origin" (p. 50). MÜLLER's general conclusions regarding the Pleistocene differentiation of the Neotropical fauna and the numerous distribution maps included in his book will stimulate further zoogeographical studies in South America. However, certain ornithological text materials should be used in connection with an appropriate source.

Additional data concerning the speciation patterns of Neotropical animals are presented in the proceedings of a recent symposium on the 'Biogéographie et Evolution en Amérique Tropicale' (Publ. Laboratoire de Zoologie, L'Ecole Normale Supérieure, no. 9, 1977, in press).

Plants.

From a botanical point of view, SIMPSON (1972) supported the assumed existence of eastern Peruvian forest refugia on evidence of Rubiaceae genera. PRANCE (1973) presented evidence to reconstruct the location of forest refugia in Amazonia based on a careful phytogeographical study of four families of Amazonian trees, viz. Chrysobalanaceae, Dichapetalaceae, Caryocaraceae, and Lecythidaceae. Most of the distribution centers analysed by PRANCE agree closely with those proposed for Neotropical animals (Fig. 10). It is encouraging to see that the results of this first study on the differentiation patterns of South American lowland forest plants also strongly support our interpretation of the history of Amazonian biota. The differentiation of the flora of the high tropical Andes has been mainly influenced by Pleistocene climatic shifts of altitudinal vegetation zones (SIMPSON 1975).

According to MOORE (1973), the distribution pattern and presumably the history of differentiation of certain Neotropical palms is similar to that of Amazonian birds. CAMP (1952: 210, footnote) noted that "The flora of the tropical South American lowlands, especially that of the Central Amazonian basin (and to a lesser extent the Orinoco basin), is highly heterogeneous, yet it is not a centrifugal flora; it is a centripetal flora, obviously having been derived (as the majority of lowland floras) from what might be called the "piedmont areas" of the surrounding uplands. Furthermore it is a recent flora, many groups being characterized by a series of often poorly delimited genera and species, apparently the result of yet active genic introgressions and unstabilized segregations." The studies of DUCKE et al. (1953) show strong provincialism of the Amazonian forest floras which may be similar to that observed in Neotropical animals (Western Hylaea, Northern Hylaea, Southern Hylaea, etc.). The area north of the lower Amazon River (Óbidos; Rio Trombetas) is of particular interest in that the flora of this region is highly heterogeneous, possibly indicating the recent rejoining of eastern and western forests.

LANGENHEIM et al. (1973) and MORLEY (1975) were critical of the refuge concept, as the distribution of the plant species studied by these authors did not closely coincide with the location of assumed refugia. However, later range expansion of the sample species may have obscured refuge boundaries. In this connection it should be emphasized that the majority of Amazonian animals also have a wide distribution and only a small portion of the species reveal the presumed location of forest refuges. We need to know the distribution pattern of a much larger percentage of the plant species composing the Amazonian flora than is presently available before a quantitative comparison with the distribution of neotropical animals and of presumed refugia is possible.

Man: MEGGERS (1974, 1975 and in press) and MEGGERS et al. (1973) presented linguistic and archeological evidence from Indian tribes, also backing the conclusions presented above. The distribution of Indian tribes in Amazonia probably was severely influenced by Late Pleistocene vegetational fluctuations. Betty Meggers' correlation of the present occurrence of Ge-Pano-Carib language people with the dispersal pattern of nonforest faunas into and across Amazonia is particularly interesting.

BROWN (1975) prepared a comparative survey of the various Neotropical forest refugia as proposed by several authors in recent years, indicating the relative importance of each refuge area and the amount of study already performed (compare also the earlier reviews of VUILLEUMIER, 1971, and VANZOLINI 1973). The more numerous and smaller forest refugia proposed by PRANCE (1973) and by BROWN et al. (1974) to explain subspeciation in butterflies and differentiation patterns in Amazonian plants may refer to a rather recent, i.e. post-Pleistocene, period of forest reduction. On the other hand, the fewer and more restricted refugia reconstructed by HAFFER and by VANZOLINI probably refer to Late Pleistocene periods of more severe aridity and a more extensive forest reduction (MEGGER, in press). Differing survival ability of animals (insects in small remnant forests, birds and mammals in larger refugia) may also explain in part the above differences of proposed forest refugia.

Amazonian nonforest bird fauna.

A number of endemic and taxonomically isolated species inhabit the unforested tableland of central Brazil south of Amazonia, such as the South American "ostrich" *Rhea americana*, the Seriema *Cariama cristata*, the Campo-Miner *Geobates poecilopterus*, and others. However, many open country bird species occur on the savannas both to the north and to the south

of the Amazonian forest. Despite the fact that these populations are separated by 2000 kilometers or more, many of them are only weakly distinct, e.g. subspecies of the flycatchers *Ma-chetornis rixosus*, *Idioptilon margaritaceiventer* and *Fluvicola pica*, of the finches *Sporophila plumbea*, *Sicalis flaveola*, *Coryphospingus pileatus* and others. This situation, as well as the comparatively low number of endemic species and the lack of endemic genera in the savanna fauna of Venezuela and eastern Colombia, indicate a rather recent direct connection of the northern and southern nonforest regions and exchange of their faunas across Amazonia (HAFFER 1967c, 1969). The same is suggested by the present existence of isolated savanna enclaves in the "dry transverse zone" of lower Amazonia through the Óbidos-Santarém region (Fig. 1). The western and eastern Amazonian forests probably had been separated more or less completely along this zone during the period 2500 to 4000 years ago as well as during earlier arid phases of the Pleistocene. The bird populations inhabiting the isolated patches of savanna vegetation within continuous forest were probably separated from their main species ranges during the most recent forest advance (approximately 2400 years ago) and some populations have since become markedly distinct, such as the parakeet *Aratinga pertinax paraensis* on a cerrado enclave near the upper Rio Tapajóz, the Brazilian flycatcher *Euscarthmus rufomarginatus savanophilus* on the Sipaliwini savanna of southernmost Surinam, the northern spinetail *Poecilurus kollari* on the upper Rio Branco savanna and many others. Similarly, the occurrence of nonforest snakes like the rattle snake, *Crotalus durissus*, on the isolated campos is indirect evidence for a former connection of these nonforest regions, as these snakes cannot be assumed to have crossed the present forest barriers (MÜLLER 1972a). The flora of the isolated Amazonian campos is decidedly non-hylaeian and resembles that of the nonforest regions north and south of Amazonia (HUECK 1966: 18, 21, 23). Botanists interpreted this situation as indicative of former forest reduction which permitted the expansion of savanna and cerrado vegetation into Amazonia.

SHORT (1975) published an important contribution to the study of the South American nonforest avifauna, analysing the relationships of the birds inhabiting the chaco region of Paraguay and northern Argentina.

Discussion

Dispersal of Amazonian birds.

The broad Amazon river and the wide lower portions of its tributaries probably represent effective barriers to the dispersal of a number of bird species inhabiting the dark forest interior, such as the trumpeters (*Psophia*, Fig. 7), many antbirds (Formicariidae), several manakins (Pipridae), and others. However, the respective allies frequently are in direct contact in the headwater region where narrow rivers cease to be barriers. Complete isolation of bird populations by rivers on all sides is observed very rarely if indeed it occurred at all. Different clinal subspecies developed rather frequently on opposite banks of widening river courses in bird species that extended their ranges downstream from the headwater region where the differences mostly resolve themselves in the parent race. Amazonian rivers merely modified or occasionally limited the dispersal of forest bird species after the latter had originated in forest refugia during dry climatic periods. In a number of medium-sized and ecologically incompatible avian species that came into secondary contact, the border of their ranges stabilized along broad river courses which, in these cases, constitute partial barriers to dispersal. In this way ecological competition is avoided.

Environmental conditions.

Evolution of the comparatively restricted Tertiary forest fauna around the old land areas of South America and along some slopes of the early "Andean" islands had probably been determined mainly by paleogeographic changes in the distribution of land and sea thus interrupting and reestablishing contact between populations. By contrast, faunal differentiation during the Quaternary was influenced by the vast expansion of dense forests into the fully emerging Amazon basin, into the lowlands and along the slopes of the rising Andes mountains during the Late Pliocene. Geological and biogeographical evidence discussed above suggests repeating reduction and expansion of the forests as a result of the Quaternary periodicity of world climates. Although a number of species composing the present Neotropical avifauna may represent direct descendants of Tertiary forms, many species have probably undergone considerable evolutionary change during the Pleistocene.

Speciation.

Numerous superspecies are found among Amazonian birds and favor the interpretation of recently completed speciation in many groups. The various allospecies composing the superspecies have achieved, or are assumed to have achieved, reproductive isolation but are still incompatible ecologically, and exclude one another geographically in continuous Amazonian forests. 76% of the jacamars (Galbulidae), 85% of the toucans (Ramphastidae) and about 75% of the Cracidae are members of superspecies (HAFFER 1974). These percentage figures are expected to be lower in Neotropical passerines, especially in insectivorous families, members of which may be able to effect sympatry somewhat more easily, although quantitative data are not available. HAFFER (1970) mapped additional superspecies of Amazonian parrots, cotingas, manakins and tanagers (Fig. 6) and SHORT (1972) discussed a superspecies of South American woodpeckers. Studying a non-random sample of 288 South American birds, mainly members of Patagonian and Andean groups, VUILLEUMIER (1972) found that, on the average, 53% are allospecies of superspecies. In this sample the latter author observed speciation phenomena less frequently in passerines (51% are members of superspecies) than in non-passerines (61%). This is surprising in view of the usual assumption of an increased evolutionary rate amongst passerine birds. Our own result of a very high percentage of superspecies in toucans (Ramphastidae) and jacamars (Galbulidae) is in line with VUILLEUMIER's finding and points out the need for comparative systematic studies of the problems involved (HAFFER 1974).

The component species of each superspecies probably originated from a common ancestor whose range was split into a number of small isolated portions during dry climatic phases of the Quaternary. Some populations may have achieved the species level of differentiation during one period of isolation whereas others, during the same interval, may have reached only the subspecies level or less depending upon the size of the refuge population, the degree of isolation, and the varying "plasticity" of systematic units. Repeated isolation of more slowly differentiating populations in their respective refugia during successive periods of forest reduction led to increasing levels of differentiation until full species status may have been reached after two or three periods of isolation. The rate of taxonomic differentiation ranges from "slow" to "rapid" and probably reached higher rates in certain groups than has been generally assumed. Under favorable circumstances, the speciation process in birds may be completed in 10 000 to 20 000 years and SELANDER (1971: 106) suggested that species occasionally may even evolve in periods of as little as a few thousand years or less. Tertiary ancestors of many Amazonian birds may have speciated repeatedly

during the Quaternary and many connecting links may have disappeared due to extinction.

The same applies to the African forest fauna which became differentiated in at least three Pleistocene refugia (Fig. 11): Upper Guinea refuge, Cameroun-Gabon refuge, and Central refuge (CARCASSON 1964, MOREAU 1966: 161, KINGDON 1971: 65). I presume that the surprising species diversity of the Neotropical forest bird fauna compared to that of tropical Africa is due primarily to more intensive speciation of the Amazonian fauna in a larger number of forest refugia distributed over a more extensive tropical lowland region than in Africa. Similar suggestions have been made by HALL (1972) and VANZOLINI (1973).

In summary, the Pleistocene differentiation of tropical and temperate faunas was probably basically similar and followed the model of geographic speciation (MAYR 1942, 1963, 1969). Pronounced changes in the vegetation cover led to the isolation of comparatively small populations in refuge areas.

Species diversity.

Important factors contributing to the high species diversity in Amazonian forests are the lack of wholesale Pleistocene extinction of animal species compared to the situation in higher latitudes, and ample opportunities for repeated geographic speciation of reduced populations in a large number of forest refugia during periods of geographic-ecological isolation (VANZOLINI et al. 1970, VUILLEUMIER 1971, MÜLLER 1972b, VANZOLINI 1973, FITTKAU 1973). Additional factors are the greater sedentariness of tropical populations, increased efficiency of physical barriers in the tropics, and the existence of narrower niches (JANZEN 1967, MAYR 1969). Increased interspecific competition, more severe predator pressure and other aspects of species-rich animal communities probably led to a reduction of niche size, i.e. increased specialization, and decreased population density of individual species in tropical forests. This development was permitted by an increasingly high plant species diversity, increased structural diversity and a more stable climate without severe winters, and resulted in the preservation of a large number of the species produced. There is no indication for the occurrence of an increased rate of mutation in the tropics or a speeding up of the number of generations which might accelerate the speciation process. Thus a fully or partial genetic interpretation of tropical species diversity seems unlikely (MAYR 1969).

The present complexity of the Amazonian forest fauna, geologically speaking, is fairly "recent" in origin and was gradually built up during the Late Tertiary and especially during the Pleistocene periods of rapid differentiation, when also massive extinction of species and entire evolutionary lines probably occurred. The traditional concept of ancient forests in the tropics, where evolution of plants and animals occurred in the absence of natural destructive catastrophes over long geological periods, has proved to be incorrect. The origin of the numerous tropical species reveals itself as a problem of historical biogeography, and the preservation and coexistence of the many species, i.e. the maintenance of the high species diversity, is due primarily to the ecological heterogeneity of tropical forests under a fairly constant humid climate.

The model of Pleistocene faunal differentiation in tropical South America discussed above may provide a conceptual framework for future regional and more quantitative studies on the evolution of Amazonian plants and animals. Detailed taxonomic investigations, studies on the population structure of Amazonian animals, and ecological field work in areas of faunal fusion and along zones of secondary contact of allied forms will be particularly revealing. TERBORGH et al. (1969, 1975) and TERBORGH (1971) have conducted studies on the distributional ecology of Andean birds in general and on the role of compe-

titution in avian distribution in particular. Hopefully, their work will be extended into the Amazonian lowlands. Long-term investigations of local avifaunas at single localities such as those of O'NEILL (1974) and O'NEILL et al. (1974) in eastern Peru will build the required data base for quantitative regional comparisons of various avifaunas of central South America.

Summary

Zoogeographical studies on distribution centers and population structure of Amazonian birds, lizards, and butterflies suggest that many subspecies and species originated from small isolated populations during several periods of ecologic-geographical separation. Repeated climatic fluctuations during the Quaternary leading to vast changes in the vegetation cover of tropical South America have been postulated by earth scientists and support the above biological interpretation. Numerous zones of secondary contact of Neotropical birds indicate the former existence of ecological barriers in Amazonia that have since disappeared. These contact zones are clustered in several well defined areas indicating that here entire faunas overlapped and partly fused, e.g. in northcentral Amazonia, in south-central Amazonia, in upper Amazonia south of the Rio Marañón, as well as in portions of the forest region west of the Andes. The ecological instability of the South American tropics during the Quaternary determined important aspects of the evolution of the Amazonian vertebrate faunas.

Forests survived arid climatic periods probably in restricted areas which served as refugia for the Amazonian forest faunas. Using indirect evidence derived from inequalities of rainfall and from avian distribution patterns I reconstructed the probable geographic location of fifteen tentatively postulated forest refugia or groups of refugia in the lowlands of Middle and South America. Differentiation of isolated populations took place in these forest refugia due to varying selection pressure, chance and "plasticity" of systematic units following the model of geographic speciation.

Large Amazonian rivers modified or occasionally limited the dispersal of forest birds from the forest refugia in reexpanding forests, especially in species inhabiting the dark forest interior. The range limit of several ecologically incompatible allies stabilized along broad river courses which, in these cases, constitute partial barriers to dispersal. In this way ecological competition is avoided. However, numerous component species of Amazonian superspecies are in direct contact and exclude one another geographically in uniform forests as a result of ecological competition.

Nonforest faunas advanced into Amazonia during periods of forest reduction, repeatedly establishing contact between the savanna faunas north and south of the Amazonian forest during the Pleistocene and post-Pleistocene. About 2400 years ago, readvancing forests led to the isolation of nonforest animal populations on savanna enclaves in the dry transverse zone of lower Amazonia.

The present complexity of the Amazonian bird fauna is fairly "recent" in origin. This suggestion probably applies generally to the faunas of the Neotropical Region.

Resumo

Estudos zoogeográficos sobre centros de dispersão e estrutura de população de aves, lagartos e borboletas amazônicas sugerem que muitas subespécies originaram-se de pequenas populações isoladas durante diversos períodos de separação ecológico-geográfica. Repetidas flutuações climáticas durante o quaternário, que conduziram a ambas modificações da cobertura vegetal da América do Sul tropical, foram postuladas por geocientistas e sustentam a interpretação biológica acima. Numerosas zonas de contato secundário de aves neotrópicas indicam a existência anterior de barreiras ecológicas na Amazônia que desde então desapareceram. Estas zonas de contato estão agrupadas em diversas áreas bem definidas, indicando que aqui faunas inteiras se sobrepuseram e fundiram parcialmente, p. ex. no centro-norte e no centro-sul da Amazônia superior ao sul do Rio Marañón, assim como nas porções

da região florestal a oeste dos Andes. A instabilidade ecológica dos trópicos sulamericanos durante o quaternário determinam importantes aspectos da evolução das faunas de vertebrados amazônicos.

As florestas sobreviveram os períodos climáticos áridos provavelmente em áreas restritas que seviram de refúgio para as faunas florestais amazônicas. Usando evidências indiretas deduzidas de descontinuidades das precipitações atmosféricas e de padrões de distribuição de aves, eu reconstruí a provável localização geográfica de quinze refúgios florestais ou grupos de refúgios, postulados a título de experiência, nas planícies da América Central e do Sul. A diferenciação de populações isoladas teve lugar nestes refúgios florestais devido à variável pressão seletiva, acaso e "plasticidade" das unidades sistemáticas, seguindo o modelo da especiação geográfica. Grandes rios amazônicos modificaram ou limitaram ocasionalmente a dispersão de aves florestais de refúgios florestais para florestas em reexpansão, especialmente de espécies habitantes do interior umbroso de florestas. Os limites de ocorrência de diversas espécies aparentadas ecologicamente incompatíveis, estabeleceram-se ao longo de grandes cursos fluviais que, nestes casos, constituem barreiras parciais à dispersão. Desta maneira a competição ecológica é evitada. Contudo, numerosas espécies componentes de superespécies amazônicas estão em contato direto e excluem-se mutuamente geograficamente em florestas uniformes como resultado da competição ecológica.

Faunas não-florestais avançaram para dentro da Amazônica durante períodos de redução florestal, estabelecendo repetidamente contato entre as faunas de savana ao norte e ao sul da floresta amazônica durante o pleistoceno e post-pleistoceno. Há cerca de 2.400 anos, o reavanço das florestas levou ao isolamento de populações animais não-florestais em "enclaves" de savana na zona transversal seca de baixa Amazônica.

A presente complexidade da fauna de aves amazônicas é de origem relativamente recente. Esta sugestão se aplica provavelmente de maneira geral as faunas de Região Neotropical.

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References

- ABSY, M.L. and T. van der HAMMEN (1977): Palaeoecological studies of Rondônia, southern part of the Amazon basin. *Acta Amazônica* 7.
- BAKKER, J.P. (1970): Differential tectonic movements and climatic changes in the mountain area of Surinam (Guyana) during the Quaternary period. *Acta Geogr. Lodziana* 24: 43-60.
- BIGARELLA, J.J. (1965): Subsídios para o estudo das variações de nível oceanico no quaternario brasileiro. *Anais Acad. Brasil.* 37 (Supl.): 263-278.
- BIGARELLA, J.J. and G.O. ANDRADE (1965): Contribution to the study of the Brazilian Quaternary. *Geol. Soc. America, Special Paper* 84: 433-451.
- BROWN, K.S. (1975): Geographical patterns of evolution in Neotropical lepidoptera. Part II: Systematics and derivation of known and new *Heliconii* (Nymphalidae: Nymphalinae). *Journ. Entomol. (B)* 44, pp. 201-242.
- BROWN, K.S. (1977): Centros de evolução, refúgios quaternarios, e conservação de patrimônios genéticos na região neotropical: padrões de diferenciação em Ithomiinae (Lepidoptera: Nymphalidae). *Acta Amazônica* (in press).
- BROWN, K.S. and O.H.H. MIEKLE (1972): The *Heliconians* of Brazil (Lepidoptera: Nymphalidae). Part II. Introduction and general comments, with a supplementary revision of the tribe, *Zoologica* (New York) 1972: 1-40.
- BROWN, K.S., P.M. SHEPPARD and J.R.G. TURNER (1974): Quaternary refugia in tropical America: evidence from race formation in *Heliconius* butterflies. *Proc. Royal Soc. London, B*, 187: 369-378.
- CAMP, W.H. (1952): Phytophyletic patterns on lands bordering the South Atlantic basin. *Bull. Amer. Mus. Nat. Hist.* 99: 205-212.
- CARCASSON, R.H. (1964): A preliminary survey of the zoogeography of African butterflies. *East African Wildlife Journ.* 2: 122-157.
- DAMUTH, J.E. and R.W. FAIRBRIDGE (1970): Equatorial Atlantic deep-sea arkosic sands and ice-age aridity in tropical South America. *Bull. Geol. Soc. America* 81: 189-206.
- DAMUTH, J.E. and N. KUMAR (1975): Amazon cone: morphology, sediments, age and growth patterns. *Bull. Geol. Soc. America* 86: 863-878.

- DORST, J. (1974): Hypothèses sur les causes de la diversification et de la richesse spécifique de l'avifaune néotropical. *C.R. Acad. Sci. Paris* 278: 2535-2540.
- DUCKE, A. and G.A. BLACK (1953): Phytogeographical notes on the Brazilian Amazon. *Anais. Acad. Brasil. de Ciências* 25: 1-46.
- DUELLMAN, W.E. (1972): South American frogs of the *Hyla rostrata* group (Amphibia, Anura, Hylidae). *Zool. Mededelingen* 47 (14): 177-192.
- DUELLMAN, W.E. and M.L. CRUMP (1974): Speciation in frogs of the *Hyla parviceps* group in the upper Amazon basin. *Occas. Papers Mus. Nat. Hist. (Univ. Kansas)* no. 23, 40 pp.
- ECHTERNACHT, A.C. (1971): Middle American lizards of the genus *Ameiva* (Teiidae) with emphasis on geographic variation. *Misc. Publ. Mus. Nat. Hist. (Univ. Kansas)* no. 55, 86 pp.
- EDEN, M.J. (1974): Paleoclimatic influences and the development of savanna in southern Venezuela. *Journ. Biogeogr.* 1: 95-109.
- FITTKAU, E.J. (1973): Artenmannigfaltigkeit amazonischer Lebensräume aus ökologischer Sicht. *Amazoniana* 4 (3): 321-340.
- FITTKAU, E.J. (1974): Zur ökologischen Gliederung Amazoniens. I. Die erdgeschichtliche Entwicklung Amazoniens. *Amazoniana* 5 (1): 77-134.
- GALLARDO, J.M. (1972): Origen de las faunas sudamericanas de anfibios. *Comunicaciones Museo Argentino de Ciencias Naturales, Zool.*, vol. 4 (4): 17-32.
- GARNER, H.F. (1959): Stratigraphic-sedimentary significance of contemporary climate and relief in four regions of the Andes mountains. *Bull. Geol. Soc. Amer.* 70: 1327-1368.
- GARNER, H.F. (1966): Derangement of the Rio Caroní, Venezuela. *Revue Géomorph. Dynamique* 2: 53-80.
- HAFFER, J. (1967a): Speciation in Colombian forest birds west of the Andes. *Amer. Mus. Novitates* 2294, 57pp.
- HAFFER, J. (1967b): Some allopatric species pairs of birds in northwestern Colombia. *Auk* 94: 343-365.
- HAFFER, J. (1967c): Zoogeographical notes on the "nonforest" lowland bird faunas of northwestern South America. *Hornero (Buenos Aires)* 10: 315-533.
- HAFFER, J. (1969): Speciation in Amazonian forest birds. *Science* 165: 131-137.
- HAFFER, J. (1970): Art-Entstehung bei einigen Waldvögeln Amazoniens. *Journ. Ornith.* 111: 285-331.
- HAFFER, J. (1974): Avian speciation in tropical South America. With a systematic survey of the toucans (Ramphastidae) and jacamars (Galbulidae). *Publ. Nuttall Ornith. Club* 14, 390 pp. (c/o Mus. Comp. Zool., Harvard Univ., Cambridge, Mass.).
- HAFFER, J. (1975): Avifauna of northwestern Colombia, South America. *Bonn. Zool. Monogr.* 7: 182pp.
- HAFFER, J. (1977): Distribution of Amazon forest birds. *Bonn. Zool. Beitr.* (in press).
- HALL, B.P. (1972): Causal ornithogeography of Africa. *Proc. XVth Intern. Ornith. Congr.*: 585-593.
- HEYER, W.R. (1973): Systematics of the *Mamoratus* group of the frog genus *Leptodactylus* (Amphibia, Leptodactylidae). *Contrib. in Science (Los Angeles Nat. Hist. Mus.)* no. 251, 50pp.
- HOOGMOED, M.S. (1973): Notes on the herpetofauna of Surinam IV: The lizards and amphihaenians of Surinam. *Biogeographica* vol. 4, 419 pp. Junk, The Hague.
- JANZEN, D.H. (1967): Why mountain passes are higher in the tropics. *Amer. Naturalist* 101 (no. 919): 233-249.
- JOURNAUX, A. (1975): Recherches géomorphologiques en Amazonie brésilienne. *Bull. Centre Géomorph. Caen (CNRS)*, 20: 1-67.
- KINGDON, J. (1971): East African Mammals. An Atlas of Evolution in Africa, vol. 1. Academic Press.
- KROOK, L. (1970): Climate and sedimentation in the Guianas. *Proc. 8th Guiana Geol. Conference, Paper* 18, 16 pp.
- LANGENHEIM, J.H. Y.-T.-Lee, and S.S. MARTIN (1973): An evolutionary and ecological perspective of Amazonian *Hylaea* species of Hymenaeae (Leguminosae: Caesalpinioideae). *Acta Amazônica* 3 (1): 5-38.
- LANNING, E.P. and T.C. PATTERSON (1967): Early man in South America. *Sci. American* 217: 44-50.
- MAYR, E. (1942): Systematics and the Origin of Species. Columbia Univ. Press, New York.
- MAYR, E. (1963): Animal Species and Evolution. Harvard Univ. Press, Cambridge.
- MAYR, E. (1969): Bird speciation in the tropics. *Biol. Journ. Linn. Soc. (London)* 1: 1-17.

- MEGGERS, B.J. (1974): Environment and culture in Amazonia. In: C. WAGLEY (ed.) *Man in the Amazon*. Univ. Presses of Florida, Gainesville, p. 91-110.
- MEGGERS, B.J. (1975): Application of the biological model of diversification on the cultural distributions in tropical lowland South America. *Biotropica* 7: 141-161.
- MEGGERS, B.J. (in press): Vegetational fluctuations and prehistoric cultural adaptation in Amazonia: Some tentative correlations. *World Archeology*.
- MEGGERS, B.J. and C. EVANS (1973): A reconstituição da pré-história amazônica. Algumas considerações teóricas. *Museu Goeldi, Publ. Avulsas* 20: 51-69.
- MILLIMAN, J.D., C.P. SUMMERHAYES and H.T. BARRETTO (1975): Quaternary sedimentation on the Amazon continental margin. *Bull. Geol. Soc. Amer.* 86: 610-614.
- MOORE, H.E., Jr. (1973): Palms in the tropical forest ecosystems of Africa and South America. In: B.J. MEGGERS et al. (eds.) *Tropical Forest Ecosystems in Africa and South America*. Smiths. Inst. Press, Washington, D.C., p. 63-88.
- MOREAU, R.E. (1966): *The Bird Faunas of Africa and its Islands*. Academic Press, London and New York.
- MORLEY, T. (1975): The South American distribution of the Memecyleae (Melastomataceae) in relation to the Guiana area and to the question of forest refuges in Amazonia. *Phytologia* 31 (3): 279-296.
- MOUSINHO, M.R. (1971): Upper Quaternary process changes of the middle Amazon area. *Bull. Geol. Soc. America* 82: 1073-1078.
- MÜLLER, P. (1972a): Centres of dispersal and evolution in the Neotropical Region. *Studies on the Neotropical Fauna* 7: 173-185.
- MÜLLER, P. (1972b): Der neotropische Artenreichtum als biogeographisches Problem. *Zool. Mededelingen* 47: 88-110.
- MÜLLER, P. (1973a): Dispersal centres of terrestrial vertebrates in the Neotropical Realm. *Biogeographica* 2, 244 pp. Junk, The Hague.
- MÜLLER, P. (1973b): Historisch-biogeographische Probleme des Artenreichtums der südamerikanischen Regenwälder. *Amazoniana* 4(3): 229-242.
- MYERS, C.W. (1973): A new genus for Andean snakes related to *Lygophis boursieri* and a new species (Colubridae). *Amer. Mus. Novitates* no. 2522, 37 pp.
- MYERS, C.W. (1974): The systematics of *Rhadinaea* (Colubridae), a genus of New World snakes. *Bull. Amer. Mus. Nat. Hist.* 153: 1-262.
- O'NEILL, J.P. (1974): The birds of Balta, a Peruvian Dry Tropical Forest locality, with an analysis of their origins and ecological relationships. Ph.D. thesis, Louisiana State University.
- O'NEILL, J.P. and D.L. PEARSON (1974): Estudio preliminar de las aves de Yarinacocha, Departamento de Loreto, Perú. *Publ. Mus. Hist. Nat. Javier Prado (Lima) ser. A (Zool.)*, no. 25.
- PRANCE, G.T. (1973): Phytogeographic support for the theory of Pleistocene forest refuges in the Amazon basin, based on evidence from distribution patterns in Caryocaraceae, Chrysobalanaceae, Dichapetalaceae, and Lecythidaceae. *Acta Amazonica* 3(3): 28 pp.
- REINKE, R. (1962): *Das Klima Amazoniens*. Dissertation, Univ. Tübingen.
- REMINGTON, C.L. (1968): Suture-Zones of hybrid interaction between recently joined biotas. *Evolutionary Biol.* 2: 321-428.
- SCHREIBER, H. (1973): Ausbreitungszentren von Sphingiden (Lepidoptera) in der Neotropis. *Amazoniana* 4(3): 273-281.
- SELANDER, R.K. (1971): Systematics and speciation in birds. In: D.S. FARNER et al. (eds.) *Avian Biology*, vol. 1: 57-147. Academic Press, New York and London.
- SHORT, L.L. (1972): Relationships among the four species of the superspecies *Celeus elegans* (Aves, Picidae). *Amer. Mus. Novitates* 2487, 26 pp.
- SHORT, L.L. (1975): A zoogeographic analysis of the South American Chaco avifauna. *Bull. Mus. Amer. Mus. Nat. Hist.* 154: 163-352.
- SILVERSTONE, P.A. (1975): A revision of the Poison-arrow frogs of the genus *Dendrobates* Wagler. *Science Bull. (Nat. Hist. Mus. Los Angeles)* 21, 55 pp.
- SIMPSON, B.S. (1975): Pleistocene changes in the flora of the high tropical Andes. *Paleobiology* 1: 273-294.
- SIMPSON, D.R. (1972): Especiación en las plantas leñosas de la Amazonía peruana relacionada a las fluctuaciones climáticas durante el Pleistoceno. Resúmenes do I Congr. Latinoamericano de Botánica, México.
- SPASSKY, B., R.C. RICHMOND, S. PEREZ-SALAS, O. PAVLOVSKI, C.A. MOURÃO, A.S. HUNTER, H. HOENIGSBERG, T. DOBZHANSKY and F.J. AYALA (1971): Geography of the sibling species related to *Drosophila willistoni*, and of the semispecies of the *Drosophila paulistorum* complex. *Evolution* 25: 129-143.
- TERBORGH, J. (1971): Distribution on environmental gradients: theory and a preliminary interpretation of distributional patterns in the avifauna of the Cordillera Vilcabamba, Peru. *Ecology* 52: 23-40.
- TERBORGH, J. and J.S. WESKE (1969): Colonization of secondary habitats by Peruvian birds. *Ecology* 50: 765-782.
- TERBORGH, J. and J.S. WESKE (1975): The role of competition in the distribution of Andean birds. *Ecology* 56: 562-572.
- TURNER, J.R.G. (1971): Studies of Müllerian mimicry and its evolution in Burnet Moths and heliconid butterflies. In: R. Creed (ed.) *Ecological Genetics and Evolution*: 224-260. Blackwell Sci. Publ., Oxford and Edinburgh.
- TUTTLE, M.D. (1970): Distribution and zoogeography of Peruvian bats, with comments on natural history. *Univ. Kansas Sci. Bull.* 49: 45-86.
- UDVARDY, M.D.F. (1969): *Dynamic Zoogeography*. Van Nostrand Reinhold, New York.
- Van der HAMMEN, T. (1968): Climatic and vegetational succession in the equatorial Andes of Colombia. *Colloquium Geographicum (Bonn)* 9: 187-194.
- Van der HAMMEN, T. (1972): Changes in vegetation and climate in the Amazon basin and surrounding areas during the Pleistocene. *Geol. Mijnbouw* 51: 641-643.
- Van der HAMMEN, T. (1974): The Pleistocene changes of vegetation and climate in tropical South America. *Journ. Biogeograph.* 1: 3-26.
- Van der HAMMEN, T., J.H. WERNER, and H. Van DOMMELEN (1973): Palynological record of the upheaval of the northern Andes: a study of the Pliocene and Lower Quaternary of the Colombian Eastern Cordillera and the early evolution of its high-Andean biota. *Rev. Palaeobot. Palynol.* 16: 1-122.
- VANZOLINI, P.E. (1970): Zoología sistemática, geografía e a origem das espécies. *Inst. Geogr., Univ. São Paulo, Teses e Monogr.* 3, 56 pp.
- VANZOLINI, P.E. (1973): Paleoclimates, relief, and species multiplication in equatorial forests. In: B.J. MEGGERS et al. (eds.) *Tropical Forests Ecosystems in Africa and South America: A Comparative Review*, p. 255-258. Smiths. Inst. Press, Washington.
- VANZOLINI, P.E. and E.E. WILLIAMS (1970): South American anoles: The geographic differentiation and evolution of the *Anolis chrysolepis* species group (Sauria, Iguanidae). *Arquivos de Zoologia (São Paulo)* 19: 1-298.
- VUILLEUMIER, B.S. (1971): Pleistocene changes in the fauna and flora of South America. *Science* 173: 771-780.
- VUILLEUMIER, F. (1972): Speciation in South American birds: A progress report. *Acta IV Congr. Latinoamer. Zool.*, vol. 1: 239-255.
- VUILLEUMIER, F. (1975): Zoogeography. In: D.S. FARNER, et al. (eds.) *Avian Biology*, vol. 5: 421-496. Academic Press.
- WIJMSTRA, T.A. (1967): A pollen diagram from the upper Holocene of the lower Magdalena Valley, Colombia. *Leidse Geol. Mededelingen* 39: 261-267.
- WIJMSTRA, T.A. and T. Van der HAMMEN (1966): Palynological data on the history of tropical savannas in northern South America. *Leidse Geol. Mededelingen* 38: 71-83.
- WINGE, H. (1972): Influência das modificações climáticas do Pleistoceno no processo de especiação do grupo críptico da *Drosophila willistoni*. *Ciência e Cultura* 24: 206 (abstr.).
- WINGE, H. (1973): Races of *Drosophila willistoni* sibling species: probable origin in Quaternary forest refuges of South America. *Genetics* 74 (Suppl.): 297-298.



Fig. 1: Distribution of humid tropical lowland forest and location of rainfall centers in Middle and South America.

Explanation: Shaded - humid forest; often semideciduous around savanna regions
Vertical stripes - areas receiving over 2500 millimeters of rain per year
Solid - Andean cordilleras and Middle American mountains over 2000 meters elevation. Heavy dashed lines delimit the "dry transverse zone of lower Amazonia" characterized by numerous isolated savanna enclaves.
Letters designate areas of paleo-ecological research (see text for details).

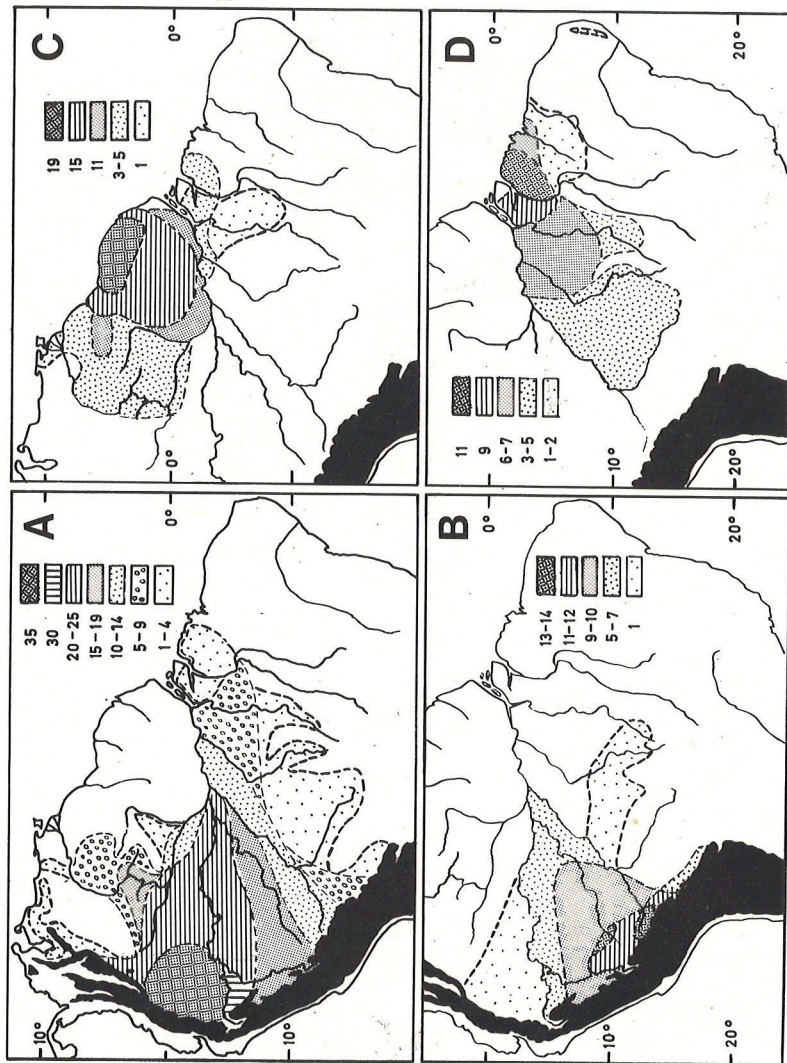


Fig. 2: Primary distribution centers of Amazonian birds.

Explanation: A, upper Amazonia (Napó center); B, eastern Peru (east Peruvian center); C, northeastern Amazonia (Guiana center); D, southeastern Amazonia (Pará center). Figures indicate number of species in sample mapped. From Haffer, 1974.



Fig. 3: Distribution and hybridisation in the Channel-billed Toucan, *Ramphastos vitellinus*.

Explanation: Character indices are contoured by isoscores (lines connecting populations with equal character index). See text for details. Mountains over 2000 meters elevation are in black. Plumage colors are rendered as follows: Solid - black; hatched - red; dotted - yellow; stippled - blue. Iris is brown in the two northern forms and blue in *ariel*. From Haffer, 1974.

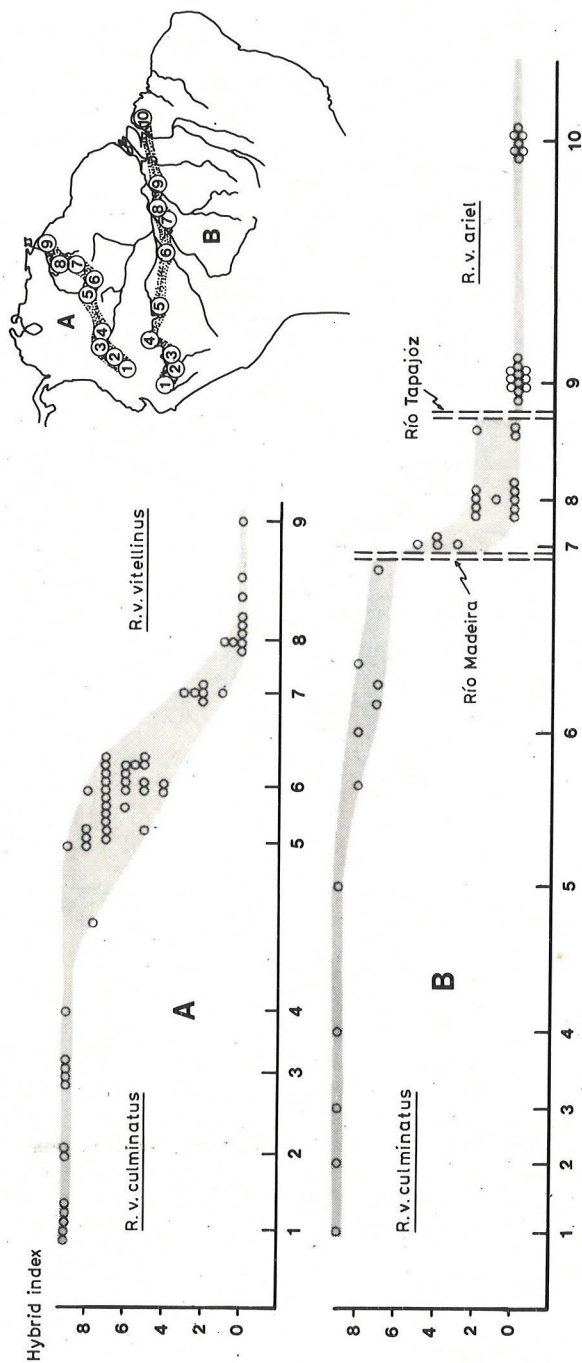


Fig. 4: Hybrid index gradient of the Channel-billed Toucan, *Ramphastos vitellinus*, in northern Amazonia (A) and central Amazonia (B).

Explanation: Each symbol represents one specimen. Note the steep continuous intergradation through highly variable hybrid populations in southern Venezuela (A). A segmented hybrid zone is present near the south bank of the Amazon River (B) where the broad lower portions of the Rio Madeira and Rio Tapajóz hinder gene flow considerably. From Haffer, 1974.

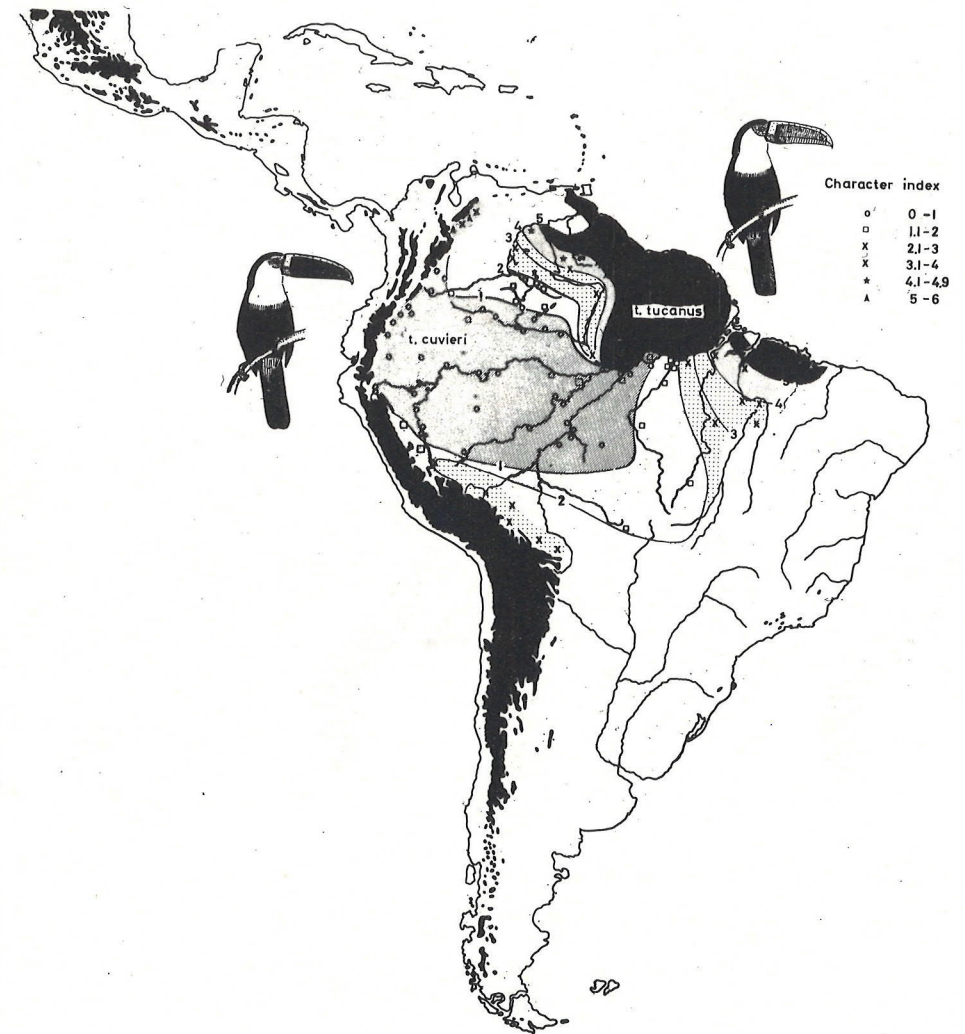


Fig. 5: Distribution and hybridization in the White-throated Toucan, *Ramphastos tucanus*.

Explanation: Index values of bill color have been contoured, see text for details. Color key: black (solid), white (blank), red (dashed), yellow (dotted), blue (stippled). The iris is brown in both subspecies. Andes mountains over 2000 meters elevation are in black. From Haffer, 1974.

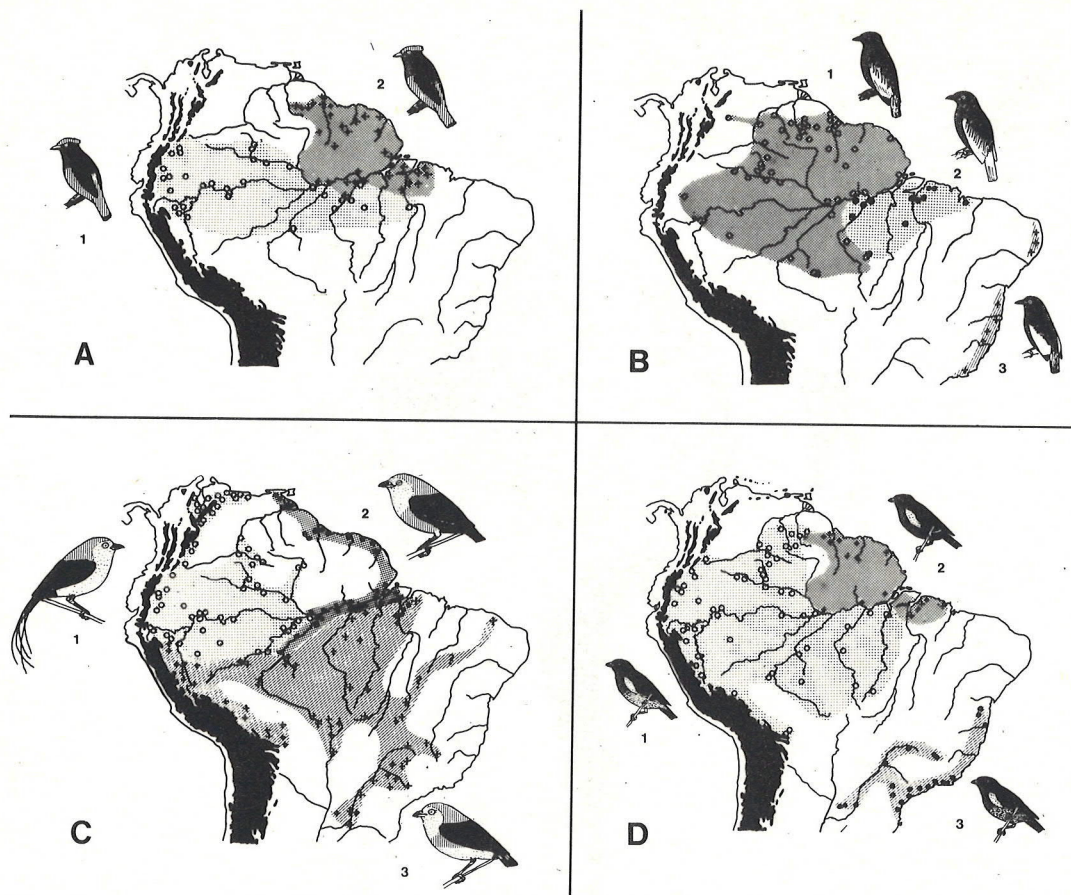


Fig. 6: Superspecies of Amazonian forest birds.

- Explanation: A *Phoenicircus carnifex* superspecies (1 *P. nigricollis*, 2 *P. carnifex*), hatched - red
 B *Xipholena punicea* superspecies (1 *X. punicea*, 2 *X. lamellipennis*, 3 *X. atropurpurea*), plumage color is dark purple with white wings and pink or white tail
 C *Pipra aureola* superspecies (1 *P. filicauda*, 2 *P. aureola*, 3 *P. fasciicauda*), plumage black (solid), red (hatched), and yellow (stippled)
 D *Euphonia cayennensis* superspecies (1 *E. rufiventris*, 2 *E. cayennensis*, 3 *E. pectoralis*), plumage color steel blue and black (solid), rufous or chestnut (stippled)

Andes mountains over 2000 meters elevation are in black. Modified from Haffer, 1970.



Fig. 7: Distribution of the Trumpeters, *Psophia crepitans* superspecies.

- Explanation: Solid triangles - *P. c. crepitans*
 Open stars - *P. c. napensis*
 Solid stars - *P. c. ochroptera*
 Open squares - *P. leucoptera*
 Crosses - *P. v. viridis*
 D - *P. v. dextralis*
 I - *P. v. interjecta*
 Open circles - *P. v. obscura*

Symbols in parentheses indicate sight records. Mountains above 2000 meters elevation are in black.



Fig. 8: Distribution of the Green Jacamars, *Galbula galbula* superspecies.

Explanation: Open squares - *G. galbula*

Stars - *G. r. ruficauda* (only peripheral records are shown. Includes the ranges of the clinal forms *G. r. brevirostris* and *G. r. pallens*)

Solid triangles - *G. r. rufoviridis* and *G. r. heterogyna* in eastern Bolivia.

Open circles with center cross - *G. cyanescens* (cy)

Open circles - *G. tombacea* (to.)

Crosses - *G. pastazae* (pa)

Plumage color is mostly metallic green (hatched) and rufous (stippled). Mountains above 2000 meters elevation are in black.



Fig. 9: Pleistocene forest refugia as centers of differentiation in Amazonian forest birds and location of secondary contact zones.

Explanation: Dark shading - forest refugia

Letters indicate: G - Guatemala refuge

C - Costa Rica refuge

D - Dulce refuge

CH - Chocó refuge

N - Nechí refuge

CA - Catatumbo refuge

M - Madeira-Tapajós refuge

Light shading - humid tropical lowland forest.

Series of small open circles indicate location of secondary contact zones.

Open arrows denote expanding forest faunas.

1 - Northcentral Amazonian suture zone

2 - Southcentral Amazonian suture zone

3 - Upper Amazonian suture zone

4 - Panamá-northwestern Colombian suture zone

Mountains above 2000 meters elevation are in black

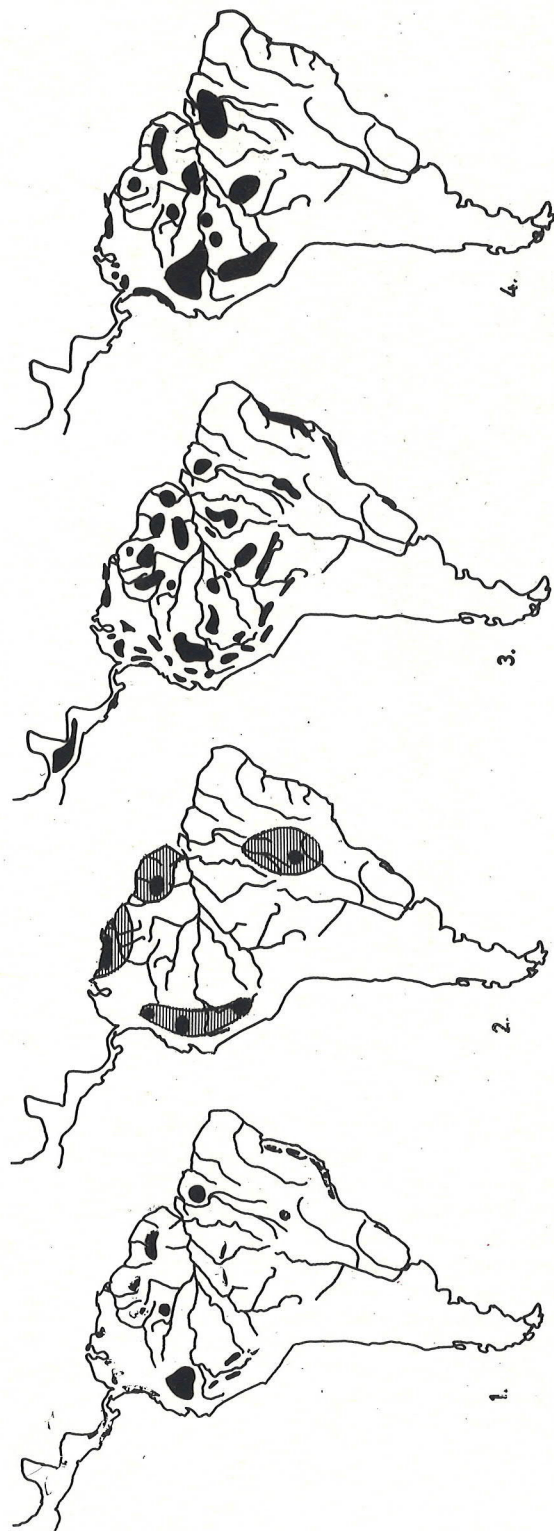


Fig. 10: Location of presumed forest refugia (black) in the Neotropics during dry climatic periods of the Pleistocene.

Explanation: 1 - Reconstruction based on distribution patterns of neotropical birds (Haffer 1967a, 1969, 1974)
 2 - Based on the population structure of Amazonian reptiles (*Anolis chrysolepis* group; Vanzolini 1970, Vanzolini et al. 1970); refugia black, core areas hatched
 3 - Based on an analysis of *Heliconius* butterflies (Brown et al. 1974, Brown 1975)
 4 - Based on a distributional analysis of four families of Amazonian trees (Prance 1973)



Fig. 11: Distribution of humid tropical lowland forest in the Neotropical Region and in Africa (shaded).

Explanation: Dark shading indicates the location of presumed forest refugia during arid climatic phases of the Pleistocene. Note more extensive forests and more numerous refugia in Middle and South America.